Population dynamics of red tide dinoflagellates

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Abstract

Sea-surface discolorations due to high concentrations of phytoplankton are called red tides. Their ecological significance is a long standing puzzle, and they are sometimes considered pathological. Here we propose that many red tides, particularly but not exclusively those comprised of certain autotrophic dinoflagellates, are presexual/sexual swarms, essential links in their complex life cycles. This view provides a rationale for the appearance of these organisms in thin surface layers, and helps explain their ephemeral nature. We suggest that further understanding of this phenomenon, and of phytoplankton ecology in general, would benefit from attention to the 'net reproductive value' (r) over the whole life cycle as well as to the division rate (μ) of the vegetative phase. It is argued that r is strategically adapted to seasonal cycles and long term environmental variability, while μ reflects tactical needs (timing) and constraints (grazers, parasites) on vegetative growth.

Key words: Red tides, Harmful algal blooms, growth, reproduction

Introduction

The appearance of high biomass single species algal blooms at the water surface, called red tides, is frequently both sudden and unanticipated, and these events normally remain visible for only a few days. In some species, these blooms are only reported at time intervals of several years. Sweeney (1975) lists eleven red tides in Southern California waters in a period of 34 years, all due to either *Lingulodinium polyedrum* (as *Gonyaulax polyedra*) or, less commonly, *Prorocentrum micans*; Omand et al (2011) provide a detailed account of the interaction of physical and biological processes leading to these *L. polyedrum* blooms. Sweeney's time series also illustrates that the diversity of red tide species is low, and that members of a rather restricted list of dinoflagellates cause most of these events (reviewed by Sournia 1995). These surface manifestations may represent only small fractions of the blooms they reveal, with most of the biomass at depth (e.g., Omand et al 2011). The apparent irregularity and ephemeral nature of red tides have historically frustrated detailed observation as well as theoretical understanding. Monitoring programmes are now relieving the first problem, although Allen (1941) considered a period of 20 years too short to establish annual patterns; something like 50 years may be nearer the mark (Dickson 1995). Modeling and prediction still present major challenges. Here we suggest that theoretical understanding of red tides can be advanced by attention to life histories. A similar case has recently been made for zooplankton (Varpe 2012).

Red tide census data have red spectra, meaning the temporal variance in abundance is concentrated at lower frequencies than in other kinds of phytoplankton bloom (Wyatt 1995). It is especially typical that species with cysts in their life-cycles have red spectra (Zingone *et al*. 2010). Deterministic models of population dynamics do not give red spectra, except with restricted parameter values, but model spectra can be reddened by adding delayed density-dependence, age-structure, life-cycles, and environmental variability. Red noise can be visible in time series of populations in which the individuals reproduce repeatedly (*iteroparous*) but not in those where reproduction is followed by death (*semelparous*) (Kaitala and Ranta 2001). Both geophysical and census data have red spectra, and we may agree with Bakun (1966) that "organisms that place the survival of certain life-cycle stages [he refers mainly to fish eggs and larvae] directly at the mercy of the ocean-atmosphere system may automatically acquire red-noise variability in their population levels".

Like other red tide dinoflagellates (*Akashiwo*, *Alexandrium*, *Gymnodinium*, *Karenia*, *Karlodinium*, *Pyrodinium*), *L. polyedrum* has a basic haplontic life cycle (Figueroa and Bravo 2005). Typically, a brief (days to weeks) planktonic haploid phase of vegetative growth leads to gametogenesis; the gametes fuse to form diploid zygotes. Gametogenesis and syngamy take 1-2 days. The zygotes can remain motile (as planozygotes) for as long as two weeks before they transform into resting cysts (hypnozygotes) which settle to the sediment. These cysts

eventually germinate and undergo meiosis, as planomeiocytes, to reestablish the haploid phase. The ecology of planozygotes and planomeiocytes is rather obscure. In some species, cysts undergo a mandatory period of dormancy. Other (non-dinoflagellate) red tide species such as the dictyochophyte *Vicicitus globosus* (Chang et al 2012) and the raphidophytes *Chattonella* and *Fibrocapsa* (Demura et al. 2012; Imai and Yamaguchi 2012) also have complex life cycles, but the latter are diplontic like diatoms.

This is not to imply that such life cycles are a pre-requisite for red tide formation, but it seems clear that species absent from the water column for long periods (≈ year) have evolved dormancy strategies, and if this period of absence is much longer than a year, implying that not all cysts germinate at the next potentially suitable time, *extended* dormancy. These life cycles are rather like the bipartite life cycles of many other marine organisms in which we see an alternation of dispersive and benthic stages. Although we generally think of phytoplankton species with life cycles that fit this pattern as planktonic, we can equally well visualize the cysts as sedentary adults, and the clones of vegetative cells to which they give rise as planktonic gonads.

Trophic versatility

Most red tide species are obligate phototrophs, but also exhibit mixotrophy that in some cases may involve phagotrophy (Seong et al 2006, Burkholder et al 2008). These features "may contribute to their ability to form dense, often almost mono-specific blooms, and to persist at high densities under stratified, nutrient-limited conditions" (Stoecker 1999). Limitation due to scarcity of inorganic (macro-)nutrients may have been an issue that led to the selection of species with more diversified resource bases. One of the few species that forms red tides in nutrient poor oceanic waters is the cyanobacterium *Trichodesmium*, a nitrogen fixer. Mixotrophy may be especially rewarding at the sea surface where the resources provided by neuston can be exploited.

Population dynamics, growth, and fitness

Many models of phytoplankton population dynamics focus primarily on the vegetative phase of the life history; less attention has been devoted to other phases (but see Eilertsen and Wyatt 2000, Yamamoto and Seike 2003, McGillicuddy et al 2003, Villanoy et al 2006, Hense 2010). The functions of the vegetative stage are simplified, to the point where its only model rôle is to acquire resources and divide. Thus the *fundamental particles* of these models are isolated cells which divide as rapidly as external conditions allow. These cells have no memories, no life histories, and exhibit no social or sexual activities; they live in a perpetual

state of *tabula rasa*, like Java applets. *Success* is measured in terms of abundance, and all population regulation is exogenous. Population dynamics is then a relatively simple accountancy problem in which division rates and loss rates determine particle abundance, and phytoplanktonic life is an exponential progression constrained only by diffusion. More complex models add top-down controls of population growth, to give us malthusian applets. Franks (2002) reviews some limitations of these models, and stresses that different questions need different models. We focus here on the issue of what red tides are for.

In the following, N refers to population density and K to carrying capacity, as in the classical logistic model,

$$dN/dt = rN(1 - N/K)$$

where r is the population growth rate. The meaning of r in this model is ambiguous, since the life cycle is ignored. The eggs, larvae, and juveniles of metazoans do not reproduce, but they enter the fitness equation. Here we distinguish between r, the growth rate over one or more complete life cycles, and μ, the growth rate during the vegetative phase. Dormancy, especially if extended, requires stores which must be laid down during growth (*sensu* μ), which means that resource needs exceed the amounts calculated on the basis of μ. A malthusian drive to divide until resources are exhausted does not permit provisioning for the future, hence in the idiom of game theory, cannot hedge bets (meaning take precautions to reduce risk). In this context, it is suggested that a target population density ($N^* < K$) is set by selection below the value allowed by carrying capacity (i.e., $N = K$), so as to allocate resources to less vulnerable life history stages (Wyatt 2013). It is also possible that if nutrient stores alloted to cysts are adequate, the subsequent vegetative phase will not require as much exogenous nutrient as applet models imply. The coupling of a bloom to a resource base is then no longer observable (Droop 1973).

Asexual (clonal) division is normally equated with reproduction, but might be better characterized as somatic growth, reserving the term reproduction for the sexual process. The distinction is important since *fitness* is based on all life history stages. Fitness, Fisher's (1958) 'net reproductive value' (r), is the malthusian parameter of genetics, or the intrinsic rate of natural increase in demography. For a particular genotype, r is the mean number of successful progeny produced *over the life cycle* (not μ, the division rate during the vegetative growth phase); for a population, the net reproductive value is $(r - m)$, where m is the loss rate, and depends on other phenotypes in the population and on the environment. Thus

$$r = [\lim/t \rightarrow \infty][\log (N_t) - \log(N_0)]/t$$

while

$$\mu = [\log (N_t) - \log(N_0)]/t.$$

To colonize a water body and bloom, the reproductive value of the *vegetative phase* ($\mu - m$) must be > 1. At K, ($\mu - m$) = 1, i.e., if m is constant, μ declines as the fraction of the water body available for colonization declines. The mechanism of density-dependence is not generally known but the target population density N^* provides a possible answer. These dynamics assume homogeneity when $N < K$, while K is equated with crowding and taken to be detrimental (MacArthur and Wilson 1970). The partitioning of resources between several activities, trade-offs between life-history stages, and the *threat* of K or other conditions unfavorable for continued growth indicate the need to anticipate changes in external conditions, and enter transitional stages with appropriate timing. For some species, it may be necessary to reach N^* so that life-history transitions can proceed. Behavioral formation of thin layers or red tides provides one route to this goal which is to some extent independent of division rate.

Dynamics of cyst phase

Each phase of a complex life cycle has more than one rôle. Wall (1975) lists five functions of dinoflagellate cysts, three directly linked to the demography of the planktonic phase, to inoculate the water column, to control the timing of inoculation, and to aid dispersal. The fourth function is genetic recombination, already accomplished by the planktonic phase in the life cycles sketched here. The fifth is to survive unfavorable conditions, sometimes the only rôle recognized for dormant stages: in fact it mixes at least two rôles, to overwinter, and to cope with environmental variability, as argued below. From the perspective of the cyst bank, the essential need for long-term survival is that it replenish itself. If inoculation and the consequent bloom are successful, the combination will provide new recruits to the cyst bank (Eilertsen and Wyatt 2000: Estrada *et al* 2010).

Over a single generation, or in a constant environment, selection should seek to maximize r; but over many generations and in variable environments, this is not the best strategy (Cohen 1966). The optimal times to switch between life history stages such as excystment and encystment depend on the *mean* deviations of the season in which vegetative growth is possible, not on its length. Thus an ability to exploit variable growth opportunities depends on features of the life cycle which are not obviously reflected in r, but in the longevity and excystment schedules of dormant stages. These optima cannot be triggered by ambient conditions.

The selective mechanisms which generate risk-spreading encystment and excystment schedules are not known but must be endogenous (Beaumont *et al.* 2009). Risk spreading reduces variance in expected fitness, which in turn maximizes mean fitness in an uncertain environment. Excystment is a risk since conditions may prove unsuitable for growth. Extended excystment schedules spread the risk, thus buffering environmental variability. If the environment simply fluctuates between good and bad, then the optimal germination fraction is

equal to the probability of a good year. There is then a trade-off between mean and variance in the traits/fitness equation, meaning that individuals or clones with a higher mean trait related to fitness are not necessarily favoured. In short, 'most' is not always best, if not coupled to 'when'. Presumably cyst recruitment fails if the growth phase does not reach N^* and is not followed by a red tide.

Brevity of blooms and red tides

The characteristic time scale of the vegetative phase is estimated by $1/\mu$. The μ_{max} value thus sets the initial slope of the "stock/recruitment" (S/R) relationship of the population, where S is the cyst stock, and $R = N$. This slope in turn sets the time (t^*) to reach some predetermined density (N^*) necessary to induce gametogenesis. For the vegetative stage, and for given values of m, it also sets the balance between the competing needs of containment, without which there are no blooms (Yamamoto and Okai 2000), and the dispersal necessary to offset local extinctions (Shigesada and Kawasaki 1997). The planomeiocyte stage, if it divides to yield four or more cells before inoculating the water column can also contribute to minimize t^*. Abundance/bloom formation is one means, not necessarily the only one, to (numerical) success of the vegetative phase.

Inherited variations in μ are tactical, variations in r are strategic: trade-offs must affect both, but not necessarily in parallel. A high division rate (a species μ_{max} value) might be selected for as a trait *vis a vis* other co-occurring phytoplankton, in a kind of scramble competition for nutrients (bottom-up). This is the archetypal view of spring bloom diatoms. But it might be selected more directly as a means to reach a predetermined population density (such as N^*) as quickly as possible to avoid a grazer response (top-down), (see Wyatt 2013). The appropriate time to reach N^*, say t^*, must enter the fitness equation. There is selection for mismatch, the essence of the red queen hypothesis (Van Valen 1973, Leung et al 2012); the shorter the value of t^*, the harder it is for grazers or parasites to track the population.

There are thus several ways to minimize t^*. Selection for a high μ_{max} value is one. Increase in inoculum size is another (Genovesi-Giunti et al 2006), and can be achieved by abundant cyst populations with appropriate excystment schedules, by planomeiocyte division, and, at the very local scale, by biologically controlled reduction of diffusion (Jenkinson and Wyatt 1992, Wyatt and Ribera d'Alcalà 2006) and grazing rates. With an inoculum of 10^2 cell L^{-1}, daily doubling (μ = 0.69), and no losses, a population of vegetative cells can reach 10^5 cell L^{-1} in 11 days. If these cells are evenly distributed in a 10 m water column, and now migrate into the upper metre, the concentration will reach 10^6 cell L^{-1}, sufficient to form visible patches, a red tide. At a swimming speed of 0.5 mm s^{-1}, this will take < 6 h. What might trigger such a migration is unknown, but if gametogenesis and

syngamy proceed promptly when a red tide accumulates, its ephemeral appearance is accounted for.

Horizontal and vertical scales of patchiness

Planktonic cells are often thought to be dispersed and advected passively by the local hydrodynamic regime, but this is an oversimplification. Biological means to achieve population integrity or cohesion in phytoplankton (vertical migration, thin layer formation, local environmental engineering) in turn imply the probability of some coupling between local production by the vegetative stage and recruitment to nearby cyst banks. The relative inoculation rates of local and distant vegetative populations by local and distant cyst banks determine the extent to which metapopulation units are closed or open, hence partly parameterize metapopulation dynamics.

The horizontal (sub-)mesoscales of phytoplankton blooms are of the order of kilometres. For other plankton, this scale is less than intuition suggests, e.g., from 10 to 50 km (with normal or exponential dispersal functions) for some fish larvae whose planktonic phases last much longer than the vegetative phases of red tide dinoflagellates (e.g., Paris *et al.* 2007, Puebla *et al.* 2012). These scales are familiar from satellite imagery of chlorophyll distributions, and closely linked to hydrodynamics (d' Ovidio et al 2010). The horizontal scales of thin layers, so far as they are known, are similar. But the scales of population *viscosity* (limitation of dispersal from natal region) necessary for genetic reasons (Hamilton 1964, Waples 1998) are orders of magnitude smaller; without this viscosity, outbreeding overwhelms inbreeding. It is argued that the evolution of sex is impossible in 'infinite' (i.e., non-viscous) populations (Otto 2009). The evolution of complex life cycles is equally impossible, by the same argument, in infinite populations.

Subsurface chlorophyll patchiness on vertical scales, a few cm to metres, is well established (Kiefer and Lasker 1975, Bjørnsen and Nielsen 1991, Franks and Jaffe 2008). Mitchell et al (2008), link this chlorophyll microstructure to "phytoplankton in polymer matrix hotspots" and to "motility driven clusters", the former possibly engineered by the cells themselves (Wyatt and Ribera d'Alcalà 2006), the latter recalling the swarms described in cultures by Persson and Smith (2013). The characteristic time of these features, 10-15 minutes, is compatible with grazing, infection, and nutrient uptake (Mitchell et al 2008), but too short for the business of blooming. Vertical patchiness on the same spatial scales and longer temporal scales is now well known (McManus et al 2003, Ryan et al 2005).

With respect to the horizontal scales of these layers, Mitchell et al also write: "While the lateral extent and patch generating mechanisms need further investigation, there is enough information to describe these as patches that while ephemeral may represent important structures for the survival of individual

plankton and for linking individual behavior to larger scale oceanographic processes". An important step *en route* to the latter must consider this patchiness in relation to turbulence/viscosity. Seuront et al (2010) do just this; significantly, "two species that best explained the spatial patterns of seawater elevated viscosity were also *Alexandrium tamarense* and *Prorocentrum* sp." For technical reasons, the microdistribution of phytoplankton immediately below the sea surface is poorly known. But there are strong indications that red tides are favoured by neaps, when turbulence is reduced (Pingree et al 1978, Crawford et al 1997, Trigueros and Orive 2000). In UK waters, strong tidal regimes appear to prevent *Alexandrium* blooms (Wyatt and Saborido-Rey 1993).

How to persist in a favourable place; the rôle of motility

The most obvious rôle of motility is to reach the sea surface and form a red tide, as we argue here, a prelude to sexuality. Omand et al (2011) provide a very high resolution account of an inshore *L. polyedrum* red tide (of the kind listed by Sweeney); they analyse the impact of convergence in and breaking of internal waves, and how these interact with cell motility; they point out as others have that chlorophyll is not a passive tracer of hydrodynamics, at least on the scale of their observations. Red tide species are clearly not entirely "at the mercy of the ocean-atmosphere system". But there may be more to it than that. In a *purely* diffusing world (no return circulation), automata cannot get *home* again with any reasonable probability. But in a bounded advective system, which necessarily has a return route, they may be able to do so if they can find that route and get the timing right. They then cease to be automata and can follow trajectories which are not determined entirely by hydrodynamics; to a degree, they can navigate (Squires 1996). Even the ability to reach the sea surface by phototaxis is navigation of a sort.

Motile planozygotes could also play a navigational rôle by countering passive dispersion, and homing (by chemotaxis?) on existing cyst banks. Some experiments of Tobin et al (2011) with *Heterosigma* suggest settlement is passive, but their experiments precluded the possibility of chemotaxis. Nevertheless, if μ is high enough, navigational skills may be unnecessary - losses could be offset by exuberant growth, meaning there is a trade-off between μ and navigational ability. Such a strategy however will not solve the demand for population viscosity. The progeny of a local bloom have three fates. They are lost (m), they recruit to the local cyst bank which generated them (closed recruitment), or they recruit to another part of the metapopulation (open recruitment). The cysts, once settled, do not face a diffusion problem unless sediments are scoured; μ and r are uncoupled.

Time keeping

The different stages of complex life histories must be coordinated, like the somatic and reproductive tissues of metazoans. This in turn requires communication *within* the stages, and time keeping. Swarm formation requires coordinated behaviour, short-lived gametes must appear simultaneously if they are to meet and mate. *Lingulodinium* has been a model organism for the study of circadian rhythms for several decades, and many cellular processes are known to be controlled by internal clocks (reviewed by Hastings 2007). Encystment and excystment must be appropriately timed as already discussed, and there is evidence for the involvement of an endogenous clock in the latter process (Perez et al 1998 and Matrai et al 2005 for *Alexandrium*). Mandatory dormancy itself acts as an endogenous clock (Montresor 1995).

The selection mechanisms which have led to extended dormancy are hardly known, but must involve time keeping. This adaptation raises difficult questions. How are excystment schedules programmed? Is excystment density dependent? If so, what are the mechanisms? Normalized by longevity, the two characteristics of apparent irregularity and ephemerality are typical of many pelagic organisms, not just some phytoplankton species, and even including some commercial nekton. These features suggest we are witness to specialized demographic strategies. In fact we can recognize a spectrum of phytoplankton life-history strategies (Lewis 1977; Zingone 2002) which are reflected in increasingly complex patterns of appearance of the planktonic phase. One might view delayed excystment schedules in the same light as the iteroparous spawning strategies of fish like herring or cod, which hedge against very uncertain larval phases, as in the match/mismatch hypothesis of Hjort (1914). We have called phytoplankton species with extended dormancy *seculoparous*, to emphasize the delay preceding the completion of reproduction (Wyatt and Zingone 2012).

Significance of the surface

Plankton patchiness is caused by differential gains and losses, i.e., the shifting balance between various population controls, hydrodynamics (diffusion, convergence), and to endogenous population processes including behaviour. The rates of any of these processes can change suddenly. In many zooplankton (Sinclair 1988), ephemeral concentrations or swarms are achieved behaviourally, and often precede spawning. Analogous swarming must occur in red tide species, and in general in any planktonic species with sexual reproduction, to enable gametogenesis and syngamy. What signals the time to migrate to the surface is unknown; N^* and quorum sensing may be involved but red tides are associated with low winds and neaps, and it may also be related to periods of low turbulence.

The water surface is the most obvious part of the photic zone where, by means of the ubiquitous planktonic habit of vertical migration (in combination with positive phototaxis), a 3-dimensional distribution can effectively become 2-dimensional,

hence bring about significant reductions in distances between individuals, and allow for intercellular communication, and for gametes to meet each other. On all scales, from molecular biology to landscape ecology, the biologically improbable in 3-D is facilitated in 2-D. Then the ephemeral appearances of some red tide dinoflagellates are analogous to the reproductive swarms of some metazoans (mysids, palolo worms, grunions).

Prorocentrum produces dimethylsulphoniopropionate (DMPS), a precursor of dimethyl sulphide (DMS) (Keller et al 1989) released during blooms; DMS in the atmosphere nucleates cloud condensation nuclei and is thus climatically active. So a further advantage of blooming at the surface is the possibility of aerial dispersal via lofting in aerosols (Hamilton and Lenton 1998). Other phytoplankters which form surface blooms, like *Phaeocystis* and *Emiliania huxleyi*, are also DMPS producers.

Conclusions

We suggest there is a tactical suite of traits that accounts for the sudden and transient nature of red tides, which manifest the fulfillment of their growth phase, and a strategic suite which ensures long term survival in highly variable environments, dependent on a resting stage capable of extended dormancy. Traits of the vegetative phase include control of abundance ($N^* < K$), possibly mediated chemically (quorum sensing) although bioluminescent signalling could be an alternative means of communication, so that subsequent dormant stages are provided with adequate reserves. In relatively benign (predictable) environments, these reserves perhaps last a year, or even much shorter periods. In uncertain environments where extended dormancy is necessary to ensure long term survival, these reserves may need to last for several years. Heterotrophy contributes to their acquisition. If vegetative growth proceeds to K, all cells starve, and then cannot provide for the future. The evolutionary trade-off is to balance the maximization of resource acquisition during the growth phase with the reserves needed 'down line', to *design* the optimal value of ($K - N^*$), which *in extremis* means a trade-off between rarity and bloom status. It is probably tactically advantageous to reach N^* in the shortest possible time (t^*), to avoid grazing responses. A well stocked cyst bank with an appropriate germination schedule can provide an inoculum of sufficient abundance to give a head start to bloom formation, as well as an insurance against seasons in which the bloom phase fails to reach N^*. The function of the bloom is then to create red tides which in turn replenish the cyst bank; red tides do what metazoans' gonads do.

The dynamical behaviour of biological populations is the sum of effects due to events with different frequencies (weather, hydrodynamics), but in sum red, in combination with endogenous regulation. Social control of population densities, of the timing of life-history transitions, some means to ensure a degree of population integrity, and dormancy are amongst these endogenous mechanisms.

Life-cycles with extended dormancy allow reduced variance in expected fitness, which is equivalent to maximizing mean fitness in variable environments. If an analogy, say with applets, is inexact, inferences and conclusions based on that analogy will be erroneous. O' Dor's *Law of Biology* states that chemistry and physics make the laws, and organisms seek out and exploit the loopholes in those laws. We can parody this law and say that modelers make the rules and organisms seek ways to confound these rules.

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